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# Relationships of the snake genera *Pythonodipsas* Günther and *Spalerosophis* Jan (Reptilia, Colubridae)

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Abstract. The monotypic genus *Pythonodipsas* is peculiar in various morphological respects. Similarities in head scutellation with *Spalerosophis* sp. represent convergence. The derived character states found in *P. carinata* do not corroborate a close relationship with Madagascan genera (Geodipsadini) but argue for an offset position among the Lycodontinae.

Key words. Lycodontinae, Geodipsadini, Palaearctic, Madagascar, monophyly.

The monotypic snake genus *Pythonodipsas* Günther, 1868 is represented by the Western keeled snake (*P. carinata*) of south-western Angola and western Namibia. This species is unique among Old World Colubrid snakes (Colubridae sensu Dowling 1974) in a combination of osteological characters, i. e., a peculiar maxillary dentition (3rd to 6th largest, posteriormost tooth large and grooved), a reduced number of palatine teeth[1]), and hypapophyses developed throughout the vertebral column.

Marx et al. (1982, p. 554) found *Pythonodipsas carinata* and *Spalerosophis diadema* to be "more similar to viperids than are any other species of Colubroidea [sic]". Both species have fourteen derived character states found in vipers (Viperidae). Seven presumably synapomorphic features (i. e., more than three loreals, more than three anterior temporals, eye not in contact with supralabials, dorsal head scalation with some small scales, palatine-pterygoid articulation with a saddle joint, intraspecific variation in keeling of dorsal scales, and enlarged anterior and posterior maxillary teeth) are said to be common to both *P. carinata* and *S. diadema*. Marx et al. (1982, p. 559) speculated about the monophyly of *Spalerosophis* Jan, 1865 and *Pythonodipsas* but they were unable to conclude "whether these taxa are related or convergent".

*Pythonodipsas* and *Spalerosophis* can be distinguished by the condition of subcaudals, dorsal scale row reduction, pupil shape, development of posterior hypapophyses, shape of basisphenoid and palatinum, and hemipenis. In *P. carinata*, the organ is divided (with a bifurcate sulcus). It is covered with uniform small spines arranged in regular series. In *S. diadema*, the organ is single (subcylindrical) with a simple sulcus spermaticus. There are larger basal spines and an apical ornamentation made up of denticulate calyces (Fig. 1). In *P. carinata*, the lateral head scalation is broken up, and a large scale separates the eye from the supralabials. The shields between the eyes (supraoculars, frontal) are entire. With the exception of two reduced shields bordering the supraoculars, the parietals are broken up into a number of small scales, and there may or may not be one or two small azygous shields between the prefrontals and the frontal (Broadley 1983). Among Palaearctic genera, *Spalerosophis*

[1]) Among Colubridae, low palatine teeth counts are considered a derived character state (Marx & Rabb 1972, character 48). Contrary to the arrangement figured by Marx et al. (1982), our specimen (TM 62801) has the third out of five and not the anteriormost tooth greatly enlarged.

is remarkable in having an increased number of midbody dorsal scale rows, ranging from 23 (in *S. diadema*) to 43 (in *S. microlepis*), and an advanced fragmentation of head scales (prefrontals, loreals, circumocular scales, temporals). There are a number of small scales which exclude the eye from the supralabials. Pre- and postoculars are likewise small and scale-like (forming an "ocular ring"). In *S. microlepis* (type species) and in *S. josephscortecci* (endemic to Somalia, Lanza 1964), the frontal is broken up. Furthermore, the type species is peculiar in having the internasals divided, whereas the African form has multiple supraoculars and partially divided parietals.

It has been outlined earlier (Schätti 1986b) that *S. diadema* and certain representatives of Palaearctic racers (genus *Coluber* s. l.) have identical states in four characters used by Marx et al. (1982), i. e. supralabial condition, maxillary teeth, palatine articulation, and dorsal keeling. The available evidence argues for a close relationship of the genus *Spalerosophis* with *C. hippocrepis* and allied species (Schätti 1986a). This group is distinct from other lineages of Palaearctic racers (Schätti in press) in lateral head scalation (increased number of supralabials, additional scales in the loreal and temporal region, development of posterior subocular scales with a tendency to exclude the orbit from contact with the supralabials), paravertebral scale row reduction, osteological features (e. g. basisphenoid, vertebrae), shape and ornamentation of the hemipenis, and biochemical data (protein electrophoresis). *Spalerosophis* is certainly not a good model for a hypothetical "protoviperid" (Marx et al. 1982). To conclude, there is no doubt that the similarities between *Pythonodipsas* and *Spalerosophis* in head scale fragmentation represent convergence.

The combination of character states found in *Pythonodipsas* is not paralleled in any Palaearctic snake. The presence of posterior hypapophyses, a bifurcate (centrifugal) sulcus spermaticus, and grooved posterior maxillary teeth made Bogert (1940) presume a relationship between *Pythonodipsas*, *Geodipsas* Boulenger, 1896 (with about six species distributed in Tropical Africa and on Madagascar), and *Ditypophis* Günther, 1881 (a single species from Socotra). Dowling & Duellman (1978) arrange these snakes with five Comoro-Madagascan genera[2]) in the tribe Geodipsadini (subfamily Lycodontinae). This group is recognized by a single dentition feature (i. e., grooved posterior maxillary teeth). The aglyphous Madagascan genera having hemipenis with bifurcated sulcus are grouped in the Pseudoxyrhophini (Dowling & Duellman 1978). Dowling (1969) found that the genera of Bogert's (1940) Group I (tribe Boaedontini) have paravertebral dorsal scale reductions. *Geodipsas* sp. have a single low reduction. According to Bogert (1940), the hemipenis of *Geodipsas depressiceps* is single with a bifurcate sulcus. The Geodipsadini (Dowling & Duellman 1978), however, contains forms with both low and paravertebral scale row reductions (three in *Madagascarophis*). Only *Ditypophis vivax* has both low and high scale row reductions and a hemipenis similar to the one found in *P. carinata*, i. e. bifurcate for one third of its length, and covered distally with very small spines (Parker 1949). *D. vivax* also has undivided subcaudals and a vertically elliptic pupil. The type specimen has notched parietal scales (Günther 1881, pl. 40) but this aberrant condition does not occur in seven other examples of this species (working sample). In fact, this species shares most characters (including

[2]) (i. e., *Alluaudina*, *Ithycyphus*, *Langaha*, *Lycodryas*, and *Madagascarophis*). Based on similarities in maxillary dentition (Parker 1949), the Oriental genus *Psammodynastes* is tentatively placed in the Geodipsadini.

supposedly derived features) with *P. carinata*. However, the distribution pattern of these monotypic genera is rather enigmatic and there must be serious doubt about the monophyly of the Geodipsadini. A detailed investigation of further snake genera is necessary to aid interpretation of characters and to deduce the phylogenetic relationship of *Pythonodipsas*. This peculiar genus has many derived character states (i. e. fragmented head shields, paravertebral scale row reduction, enlarged palatine teeth, peculiar hemipenis morphology etc.) which argue for an offset position among the Lycodontinae.

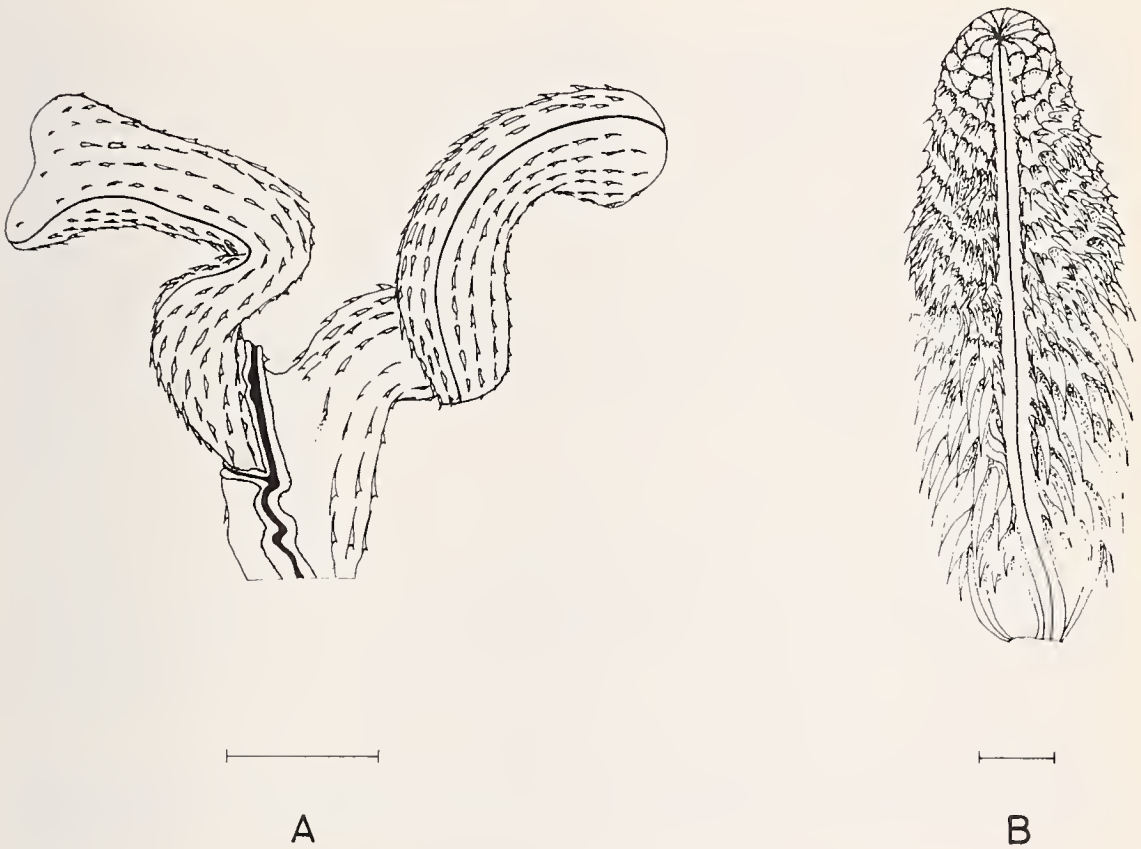


Fig. 1: Right everted hemipenis (sulcate view) of (A) *Pythonodipsas carinata* (TM 52169, broken line indicates course of sulcus spermaticus on the reverse side) and (B) *Spalerosophis diadema* (author's coll. SS 2).

**Working sample** (Geodipsadini). *Alluaudina bellyi* (Brit. Mus. [Nat. Hist.] 1948.1.7.77); *Ditypophis vivax* (BM 99.12.5.120—123, 1946.1.4.53 [type], and 1957.1.10.29—31); *Geodipsas depressiceps* (BM 1906.3.30.71); *G. infralineata* (BM 1930.2.2.14); *Ithycyphus goudoti* (BM 89.4.11.12); *Langaha nasuta* (BM 89.4.11.13; Naturhist. Mus. Basel [NHMB] 1777); *Lycodryas betsileanus* (BM 1930.2.2.15); *Madagascarophis colubrinus* (BM 1925.8.25.8; NHMB 18285); *Pythonodipsas carinata* (BM 1946.1.4.70[type]; TM 32349, 33040, 52169, and 62801).

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**Zusammenfassung**

Die südwestafrikanische Natter *Pythonodipsas carinata* unterscheidet sich in phylogenetisch gewichtigen Merkmalen klar von der paläarktischen Gattung *Spalerosophis*. Ähnliche Merkmalszustände in der Kopfbeschuppung stellen konvergente Entwicklungen dar. Am meisten Übereinstimmung (Hemipenis, Schuppenreduktion etc.) zeigt *Pythonodipsas* mit der ebenfalls monotypischen Gattung *Ditypophis* von Sokotra. *Pythonodipsas* weist eine große Zahl vermutlich apomorpher Zustände in unabhängigen Merkmalskomplexen auf. Die Geodipsadini (sensu Dowling & Duellman 1978) stellen wahrscheinlich eine polyphyletische Gruppe dar, während *P. carinata* innerhalb der Lycodontinae eine isolierte Position einnimmt.

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